BIOSYSTEMATICS OF HELIANTHUS DEBILIS[1]

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A study of the gulf coast sunflower, *Helianthus debilis,* was begun in 1946, and field work was carried on in both Florida and Texas. From the analysis of population samples and the subsequent garden cultivation of plants, it was possible to recognize nine morphological races. A systematic series of hybridizations between the races, as well as some hybridizations with other sunflower species, was carried out. Material was borrowed from several herbaria in order to supplement the author's collections. The first part of the present paper summarizes the results of the cytogenetic study, the second part deals with the taxonomy, and the final part comprises a discussion of subspeciation in these sunflowers.

HYBRIDIZATIONS

1. Intraspecific crosses. Forty-eight reciprocal crosses were made involving the races listed in Table 1. The F_1 cross was readily secured and the resulting progeny were vigorous. In general, twenty plants of each reciprocal combination were grown. As can be seen from the polygonal crossing charts (fig. 1), two distinct groups can be recognized with respect to the fertility of the F_1 hybrids. Hybrids between any two of the first six races (the "debilis" assemblage) and hybrids between any two of the last three races (the "praecox" assemblage) as a rule give highly fertile F_1 plants with around 90 per cent pollen fertility and nearly 100 per cent good seed set. Occasionally, plants with somewhat reduced fertility were encountered both in hybrids within races and between races, but their occurrence followed no consistent pattern. In general, it can be stated, then, that crosses within either the "debilis" or "praecox" assemblage of races produce fertile hybrids. However, any crosses between races of these two assemblages gave F_1 plants with pollen fertilities from 20 to 50 per cent, averaging around 30 per cent, and the seed set was one third to one half the normal amount. Only a few F_2 generations have been grown, and it has been found that those involving crosses within either assemblage give vigorous fertile plants, whereas those between the two assemblages give plants with fertilities varying from 30 to 100 per cent. In the second F_2 group, although the majority of the hybrids were vigorous, some weakness was observed in a few of the plants.

2. Interspecific crosses. Representatives of the "debilis" and "praecox" assemblages (Table 1) discussed above were crossed with several other

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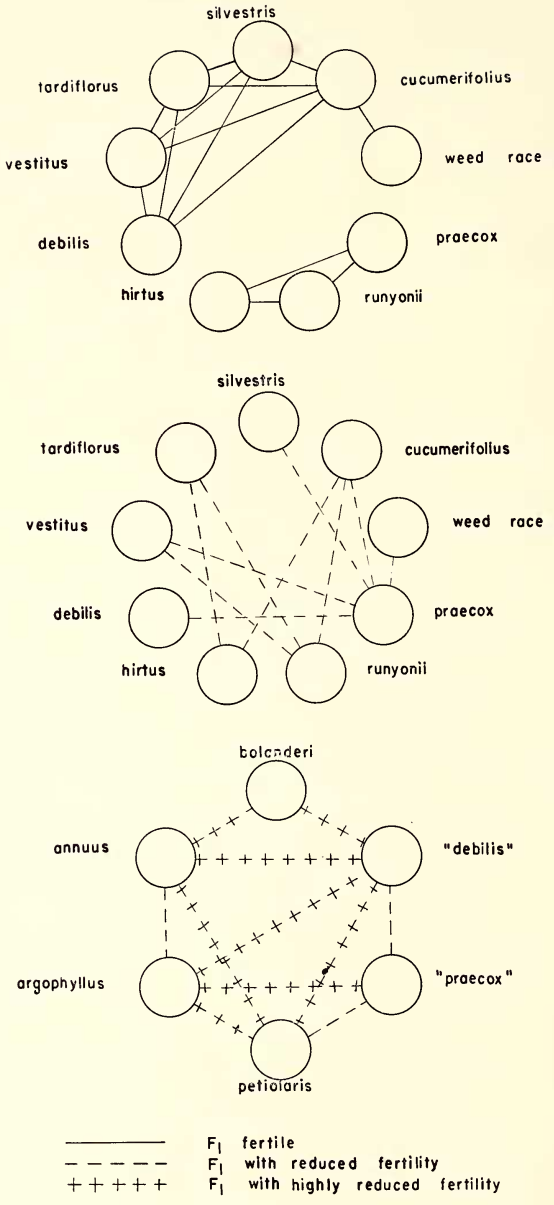

FIG. 1. Results of crosses: top, crosses of races of *Helianthus debilis* giving fertile F_1 hybrids; center, crosses of races of *H. debilis* giving F_1's with reduction in fertility; bottom, crosses involving other species of annual sunflowers. Further explanation in text.

species, and the results obtained are shown in fig. 1 (bottom). Other species crosses previously reported (Heiser, 1951) are also shown. Most interspecific crosses result in rather highly sterile F_1 hybrids with pollen fertilities generally below 20 per cent and seed set of generally less than 10 per cent. The exceptions are those hybrids between *H. annuus* and *H. argophyllus, H. petiolaris* and "praecox," and the previously mentioned hybrid between "debilis" and "praecox." Both *H. annuus* and *H. argophyllus* are partially sympatric with *H. debilis,* and natural hybrids between *H. annuus* and the latter have been found, but no natural hybridization is known between *H. argophyllus* and *H. delibis. Helianthus bolanderi* of California and Oregon does not particularly concern us in the present discussion, but is included to show that the taxa recognized as species in this group generally show considerable reduction of fertility in the F_1 hybrids. *Helianthus petiolaris,* on the other hand, and *H. debilis* are vicarious species, with *H. petiolaris* replacing *H. debilis* to the west (fig. 3). Morphologically the "praecox" assemblage appears to be intermediate between *H. petiolaris* and the "debilis" assemblage. Crosses between *H. petiolaris* and two representatives of the "debilis" assemblage give F_1 plants which fall into the highly sterile category of 20 per cent or less pollen fertility whereas crosses between *H. petiolaris* and "praecox" give F_1 hybrids with about 40 per cent pollen fertility (fig. 1).

Thus it can be seen that the "praecox" assemblage, which appears to be intermediate morphologically between *H. petiolaris* and "debilis," gives moderately fertile hybrids when crossed with these other taxa. On the other hand, hybrids between "debilis" and *H. petiolaris* show a rather great reduction in fertility, similar to those obtained in hybrids between most species of annual sunflowers.

Chromosome Numbers and Pairing

All of the annual sunflowers previously studied have been shown to possess a haploid chromosome number of 17 (Heiser, 1948). The same number has been found in all the races included in the present study. In most hybrids within races and between races belonging to either the "debilis" or "praecox" assemblages, 17 bivalents are formed at meiosis. Exceptions were noted in two crosses between races and two crosses within races of the "debilis" assemblage where some cells occurred with 17 pairs and some with 15 pairs and a chain of 4 chromosomes.

On the other hand, the hybrids resulting from crosses of races of "debilis" and "praecox" show the variable type of chromosome pairing previously reported for interspecific hybrids in *Helianthus* (Heiser, 1951). Twenty-five cells were examined in one hybrid plant from each cross and the number of pairs varied from 13 to 17. In the cells with 13 pairs, the remainder of the chromosomes generally formed two chains of four chromosomes each. Univalents were rarely observed. These configurations suggest that the two crossing groups differ by a minimum of two transloca-

tions, and in all probability the sterility observed in the hybrids is the direct result of the abnormal pairing relations.

Hybrids between "praecox" and *H. petiolaris* showed the same sort of configurations as observed in the "debilis"-"praecox" hybrid, whereas in hybrids between "debilis" and *H. petiolaris* and all of the other interspecific hybrids studied, with the exception of *H. annuus* × *H. argophyllus*, a still greater reduction in pairing at meiosis was observed.

Taxonomic Considerations

If sterility barriers develop along with morphological differences, there is no great problem in the delimitation of taxonomic categories (see Clausen, 1951), but sterility and morphological difference do not go hand in hand in *H. debilis*. The greatest morphological difference within this species is between the Atlantic Coast race of Florida and the other races of the species, whereas the gap based on crossing relationships falls between the "debilis" assemblage and the "praecox" assemblage. In Texas there is considerable difficulty in distinguishing certain "debilis" races from "praecox " races. If a purely morphological species definition were employed, two species might be recognized—the "debilis" race of east Florida constituting one species and all the other races constituting the second species. If reduction in fertility in the F_1 hybrid were used as the major criterion of species separation, two quite different species would be recognized—*debilis* and *praecox*. A compromise proposal might result in the creation of either one or three species in this complex. However, if only one species were to be recognized, then *H. petiolaris* would have to be included in it both on morphological grounds and crossability relations. Any one of the above proposals could be justified and there appears to be no one completely satisfactory solution to species delimitation in this group. Whatever course is adopted does not alter the true evolutionary relation, and for the present it is proposed to recognize the whole assemblage of "debilis" and "praecox" races as a single species. This solution, fortunately, does not result in any radical departure from current taxonomic treatments of this group. The problem of the proper treatment of *H. petiolaris* will have to be deferred until a more thorough analysis of its variation has been undertaken, and for this reason no formal taxonomic treatment of it will be attempted here.

A second problem is what taxonomic recognition, if any, should be given to the races. Thus far in the discussion the term race has been used to refer to populations or series of populations which replace each other geographically and at the same time show conspicuous morphological differences. Within each of these races it is possible to recognize "sub-races." The best example is in "tardiflorus" in which three large, geographically isolated populations were studied and showed recognizable morphological differences. It is possible also that races which appear very distinct to one who has been working with a group intensively may appear of minor significance to others. As Dobzhansky and Epling (1944) point out, it is a mat-

ter of expedience, judgment, and conventions which prevail among students at a given time as to how a species is broken up taxonomically. It seems desirable at present to give recognition to eight of the races listed in Table 1.

TABLE 1. CROSSES ATTEMPTED BETWEEN RACES OF *H. debilis*

Race	No.	Source	Herbarium specimen*	Crossed with race number
"DEBILIS" ASSEMBLAGE				
debilis (Florida)				
	21	Marineland, St. John's Co.	3179	6, 7, 13
	20	Flagler Beach, Flagler Co.	Godfrey 50894	17, 21
	19	Melbourne, Brevard Co.	3185	2, 4, 10, 11
	17	Surfside, Dade Co.	3189	20, 13
vestitus (Florida)				
	16	Long Beach, Sarasota Co.	3198	13
	15	Anna Maria Key, Manatee Co.	5215	13
	14	Indian Rocks Beach, Pinellas Co.	3207	13
	13	Clearwater, Pinellas Co.	3209	2, 3, 5, 7, 9, 10, 11, 14, 15, 16, 21
tardiflorus (Florida)				
	12	Sarasota, Sarasota Co.	3200	10
	11	Cedar Key, Levy Co.	3211	3, 6, 7, 9, 10, 13, 19
	10	Carabelle, Franklin Co.	3221	1, 2, 3, 5, 6, 7, 11, 13, 19
weed race				
	8	Augusta, Richmond Co., Ga.	4931	3, 4, 5, 7, 9
	9	Belvedere, Aiken Co., S. C.	3175	8, 11, 13
silvestris (Texas)				
	2	Nacogdoches, Nacogdoches Co.	3086	1, 3, 4, 7, 13, 19
	1	Grapeland, Houston Co.	3048	2, 10
cucumerifolius (Texas)				
	4	Frio, Dilley Co.	3068	2, 3, 5, 6, 8, 19
	3	Westhoff, DeWitt Co.	3074	2, 4, 5, 7, 8, 10, 11, 13
"PRAECOX" ASSEMBLAGE				
praecox (Texas)				
	5	Galveston Island, Galveston Co.	3080	2, 3, 5, 6, 8, 10, 11, 13, 21
runyonii (Texas)				
	6	Yturria, Willacy Co.	Runyon 4365	4, 5, 7, 10, 11, 21
hirtus (Texas)				
	7	Carrizo Springs, Dimmit Co.	3064	3, 4, 6, 7, 8, 10, 13

*All specimens except where otherwise noted were collected by the writer.

Taxonomic History

Helianthus debilis was described in 1841 by Nuttall from material collected in Florida, and a year later Torrey and Gray described *H. cucumerifolius* from Texas. In 1847 Engelmann and Gray described *H. praecox,* also from Texas. In his Synoptical Flora, Gray reduced *H. praecox* to synonymy under *H. debilis* and treated *H. cucumerifolius* as a variety of the species. Watson (1929) in his study of the genus recognized *H. debilis* and *H. cucumerifolius* and described another species, *H. vestitus,* from western Florida without indicating its relationship to either of the other species. In the recent edition of Gray's Manual, Fernald (1950) treats *H. debilis* as a species with one variety, *H. debilis* var. *cucumerifolius.*

Material from the following herbaria was seen during the course of the study: University of California, Chicago Natural History Museum, University of Georgia, University of Florida, Gray Herbarium of Harvard University, Michigan State College, Missouri Botanical Garden, New York Botanical Garden, Pomona College, Southern Methodist University, University of Texas, and Texas A. & M. College. I should like to extend my thanks to the curators of these herbaria for the privilege of studying this material. In the taxonomic treatment which follows, only the type specimen, one widely distributed specimen, and such others as are necessary for the discussion are cited. The distribution of the various taxa is shown in the maps. A mimeographed list of exsiccatae has been prepared and will be sent upon request to those interested.

The sunflowers to which *H. debilis* appears most closely related are for the most part annual species with alternate leaves and purple disk flowers. In the key given here all of the species in this group which are found in the area from east central Texas to Florida are included; however, only *H. debilis* will be treated in detail in the part which follows.

Key to Species

Phyllaries over 4 mm. wide; heads 2.5 cm. in diameter or greater; leaves usually cordate; plants commonly 1.5 m. or more tall.

Leaves, phyllaries, and stems with dense silvery white tomentum; in sandy soils; east coastal Texas, naturalized in Florida and also in cultivation ..... *H. argophyllus* T. & G.

Leaves, etc., merely hispid; rarely on sand; wide-spread weed and cultivated plant ..... *H. annuus* L.

Phyllaries 4 mm. or less wide; heads less than 2.5 cm. in diameter; leaves cuneate, truncate, or cordate; plants 2.0 m. or less tall.

Leaves lanceolate with a few prominent white hairs near base; plants commonly 1.0 to 2.0 m. tall; in wet soils; south-central Florida..... *H. agrestis* Pollard

Leaves deltoid-lanceolate without prominent white hairs; plants commonly less than 1.5 m. tall; in sandy soils.

Leaves usually entire, generally twice as long as broad, bluish-green; tips of pales in center of disk densely villous; Western United States and Northern Mexico, naturalized in East..... *H. petiolaris* Nutt.

Leaves entire or more often serrate, generally less than twice as long as broad, not bluish-green; tips of pales villous to merely hispid..... *H. debilis* Nutt.

KEY TO SUBSPECIES OF HELIANTHUS DEBILIS

Stems prostrate or nearly so; peduncles usually less than 20 cm. long; coastal regions.
Leaf serration irregular; stems usually conspicuously white-hirsute; rays seldom over 1.6 mm. long; disk diameter less than 1.2 cm. (at anthesis of the outer row of disk flowers); west Florida ..... 2. *H. debilis* subsp. *vestitus*
Leaf serration fairly regular, shallow; stem glabrous, hispid, or hirsute.
Stems completely prostrate, glabrous or hispid; rays less than 2 cm. long, yellow; east Florida ..... 1. *H. debilis* subsp. *debilis*
Stems semi-prostrate, hispid-hirsute; rays usually 2 cm. or more long, orange-yellow; bracts about 3 cm. wide; Galveston Island and adjacent mainland, Texas ..... 6. *H. debilis* subsp. *praecox*
Stems erect; peduncles usually over 15 cm. long; coastal and inland.
Phyllaries mostly 2.5–4.0 mm. broad, rarely long attenuate; stems hispid to hirsute; leaves usually with constriction near middle (fig. 6).
Branches horizontal or ascending; stems not densely hispid-hirsute; tips of central pales of the chaff seldom villous; Galveston Island and adjacent mainland, Texas ..... 6. *H. debilis* subsp. *praecox*
Branches ascending; tips of central pales of the chaff usually villous.
Stems hirsute but not densely so; peduncles seldom longer than 30 cm.; leaves seldom longer than 8 cm.; rays usually fewer than 14; southern Texas ..... 7. *H. debilis* subsp. *runyonii*
Stems densely hirsute or hispid-hirsute; peduncles usually 30–40 cm. long; leaves frequently 8–9 cm. long; rays usually 14 or more; Carrizo Springs, Texas ..... 8. *H. debilis* subsp. *hirtus*
Phyllaries usually 2.0–2.5 mm. broad, usually long-attenuate; stems glabrous or sparingly hispid; leaves gradually tapering from base to tip (fig. 6).
Lower leaves usually large, blade over 8 cm. long; peduncles very slender, 20–40 cm. long; disks relatively small, seldom over 1.5 cm. at anthesis; northeastern Texas chiefly in oak-pine woods ..... 4. *H. debilis* subsp. *silvestris*
Lower leaves smaller, blade seldom over 9 cm. long; peduncles not conspicuously slender, disks 1.4–2.0 cm. broad at anthesis.
Peduncles 25–50 cm. long; leaf serration usually shallow, fairly regular; rays usually 2 cm. or more long; disks usually 1.6 or more in diameter at anthesis; south central Texas ..... 5. *H. debilis* subsp. *cucumerifolius*
Peduncles seldom over 25 cm. long; leaf serrations usually deep, irregular; rays usually less than 2 cm. long; west and north coastal Florida. ..... 3. *H. debilis* subsp. *tardiflorus*

1. HELIANTHUS DEBILIS subsp. **debilis.**[2] *Helianthus debilis* Nutt. Am. Phil. Soc., N.S. 7:367. 1841.

Annual or perennial, prostrate, stem and branches subglabrous to densely hispid; leaves irregularly shallowly serrate to nearly entire, blade glabrous to hispid, 3.0–10.0 cm. long, 2.0–8.0 cm. wide; peduncles generally 10–20 cm. long; disk 1.1 to 1.4 cm. in diameter at anthesis; phyllaries

[2] *Helianthus procumbens* Raf. (Fl. Ludovic. 70. 1817) has been provisionally considered as synonymous with *H. debilis* Nutt. (Merrill, E. D. Index Raf. 237. 1949). This plant was observed by Robin presumably in what is now Louisiana or from the neighborhood of Pensacola. *Helianthus debilis* subsp. *debilis* does not occur in this region and *H. debilis* subsp. *tardiflorus,* which might be found near Pensacola, is not procumbent. Moreover, *H. debilis* does not have the opposite leaves described by Rafinesque for his *H. procumbens.* In any event *H. procumbens* Raf. is a later homonymn of *H. procumbens* Pers. (Syn. ii. 475. 1807). Rafinesque's species might be *Spilanthes repens* Michx.

about 2 mm. wide, short-attenuate, sometime squarrulose; rays 11–17, 1.2–2.0 cm. long, 0.5–1.0 cm. wide, yellow; central pales slightly hispid.

Distribution and citation. Common on sandy beaches from St. John's County to Dade County, Florida (fig. 2). Apparently an introduction at Key West and Lake City, Florida and in Cuba. Brevard County: *Curtis 1441.*

Type. *Baldwin,* "E. Fla.," BM, not examined (photograph from GH, and US examined).

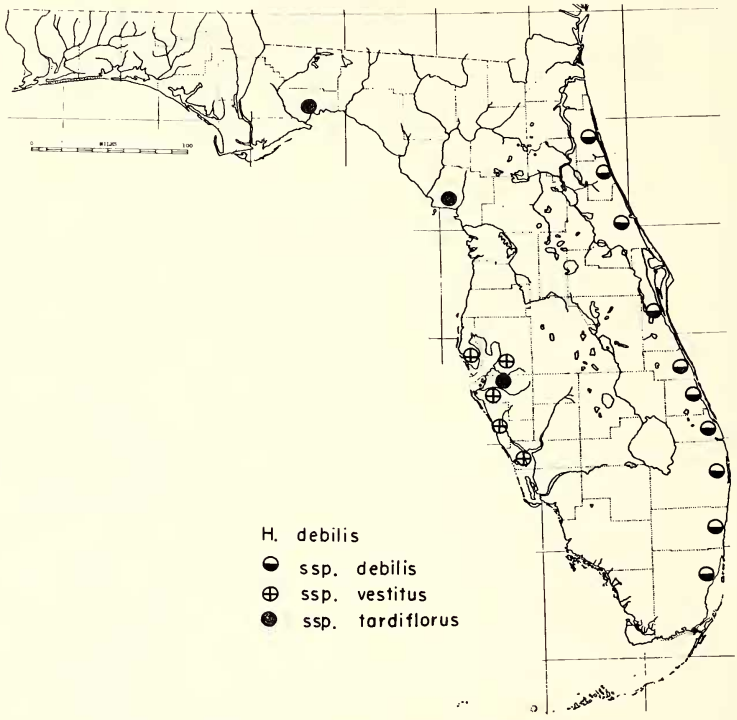

Fig. 2. Distribution of *Helianthus debilis* in Florida. (Base map through the courtesy of Dr. H. B. Sherman.)

This subspecies is very distinct and well set off from its nearest relative which appears to be subsp. *vestitus. Helianthus debilis* subsp. *debilis* is geographically isolated from other sunflowers, except *H. argophyllus,* which is naturalized in Volusia County. No evidence of hybridization between these two taxa was found.

The susbpecies is quite common on the keys of eastern coastal Florida and is rare even a short distance inland, although it is planted in yards at a number of localities in eastern Florida. The subspecies forms more or less continuous large populations in both the northern and southern parts of its range. However, in Indian River, St. Lucie, and Martin counties the populations are smaller and it seems possible that gene flow is cut down

in this area. If populations from the northernmost part at Marineland are compared with southern ones from Surfside (fig. 6), the plants appear different enough to warrant subspecific distinction, but if a series of populations from north to south is studied it is found that the variation in disk diameter, leaf length (fig. 4), and pubescence (Table 2) is in the nature

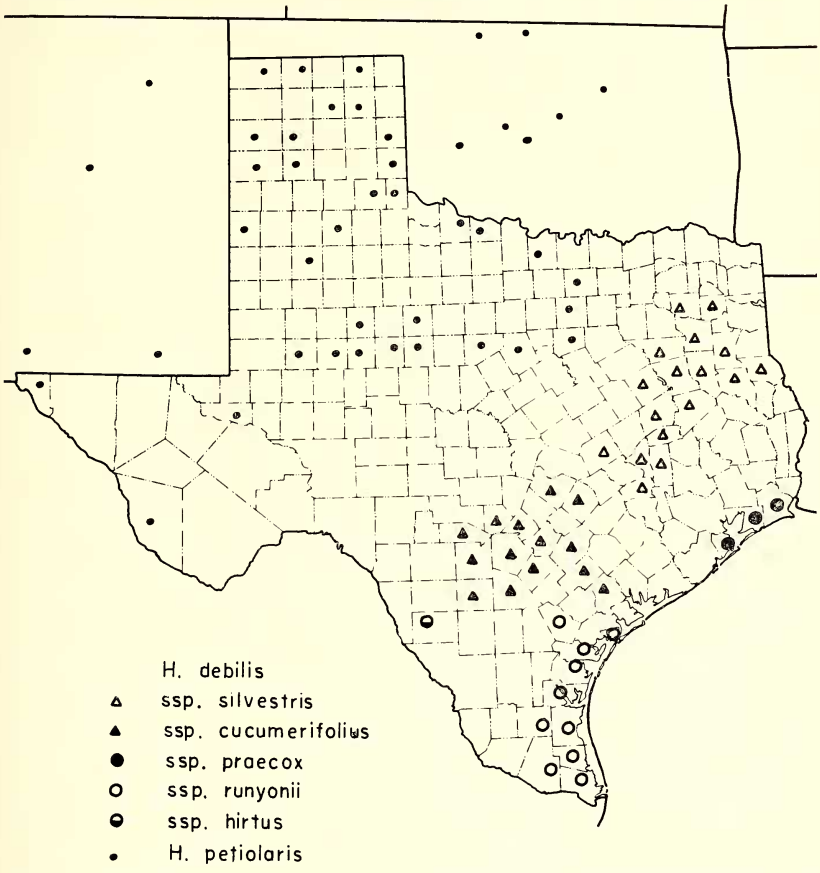

FIG. 3. Distribution of *Helianthus debilis* in Texas. The distribution of *H. petiolaris* (small dots) is given for Texas, Oklahoma, and a part of New Mexico. The latter species extends from Manitoba and Minnesota to Washington and south to northern Mexico. (Base map of Texas through the courtesy of Dr. Lloyd Shinners.)

of a cline. The leaves of the northern populations are more generally entire and cuneate whereas those from the southern counties are serrate and more frequently truncate (fig. 6). However, certain other characters, such as number and length of rays and peduncle length, do not show any significant trends. That this variation pattern is not merely ecological modification is clearly evident when comparisons are made with plants grown in the experimental garden (second column, fig. 4). The same general trend of variation is seen in the experimental garden populations, although the

measurements for certain characters do not agree with those from plants in nature. In view of these data, however, it appears that the analysis of variation in nature in *Helianthus debilis* is reliable, although Clausen (1951) has implied that the analysis of natural variation is untrustworthy because of ecological modifications in many environments. In Florida subsp. *debilis* flowers throughout most of the year. At Bloomington plants started indoors in March come into bloom the first of July.

TABLE 2. VARIATION IN LEAF PUBESCENCE IN H. DEBILIS SUBSP. DEBILIS FROM NORTH TO SOUTH FROM NATURAL AND GARDEN POPULATIONS*

Collection number*	Source	Number of plants glabrate	hispid
3179	Marineland, St. Johns County	20	0
5221	Marineland, St. Johns County	18	0
5220	Flagler Beach, Flagler County	23	0
3185	Melbourne Beach, Brevard County	20	0
5219	Melbourne Beach, Brevard County	20	2
3187	Palm Beach, Palm Beach County	18	2
5218	Palm Beach, Palm Beach County	11	8
3189	Surfside, Dade County	9	11
5217	Surfside, Dade County	4	18

* The 3100 series was collected in nature, and the 5200 series was grown in the Experimental Garden at Bloomington, Indiana.

2. HELIANTHUS DEBILIS subsp. **vestitus** (E. E. Wats.) stat. nov. *H. vestitus* E. E. Wats. Pap. Mich. Acad. 9:347. 1929.

Annual or perennial, stem rather densely hirsute with whitish hairs, main stem erect or semi-erect to 30 cm. tall, lateral branches becoming decumbent; lower leaves deltoid-lanceolate to deltoid-ovate, usually cordate or truncate, rarely cuneate at base, irregularly serrate, occasionally somewhat undulate, 4.0–8.0 cm. long, 2.5–6.0 cm. wide; peduncles 9–15 cm. long, usually hirsute; disk 1.1–1.2 cm. in diam. at anthesis; phyllaries 1.5–2.0 mm. wide, short-attenuate; rays 12–15, 1.2–1.6 cm. long, 0.6–0.7 cm. broad, yellow-orange; central pales hispid.

Distribution and citation. Known only from the keys off west central Florida from Pinellas County to Sarasota County (fig. 2). Manatee County: *Cuthbert 1445*.

Type. Hog Island (now Caladesi), Pinellas County. *Tracy 6919*, MSC.

Variation. This subspecies has at maturity a prostrate habit and in that respect resembles subsp. *debilis* and subsp. *praecox*. However, it does

EXPLANATION OF FIGURE 4

FIG. 4. Variation in leaf length of *Helianthus debilis* subsp. *debilis* from north to south in Florida. On the left are shown histograms from four population samples from Florida; on the right are shown histograms from seven populations grown in the experimental garden at Bloomington. The leaf length is given on the horizontal axis. The number of individuals in each population ranges from 17 to 24. The collections or seeds come from the following localities: *3179, 5221,* Marineland, St. John's County; *5220,* Flagler Beach, Flagler County; *5423,* Daytona Beach ,Volusia County; *3185, 5219,* Melbourne Beach, Brevard County; *5425,* Stuart, Martin County; *3187, 5218,* Palm Beach, Palm Beach County; *3189, 5217,* Surfside, Dade County.

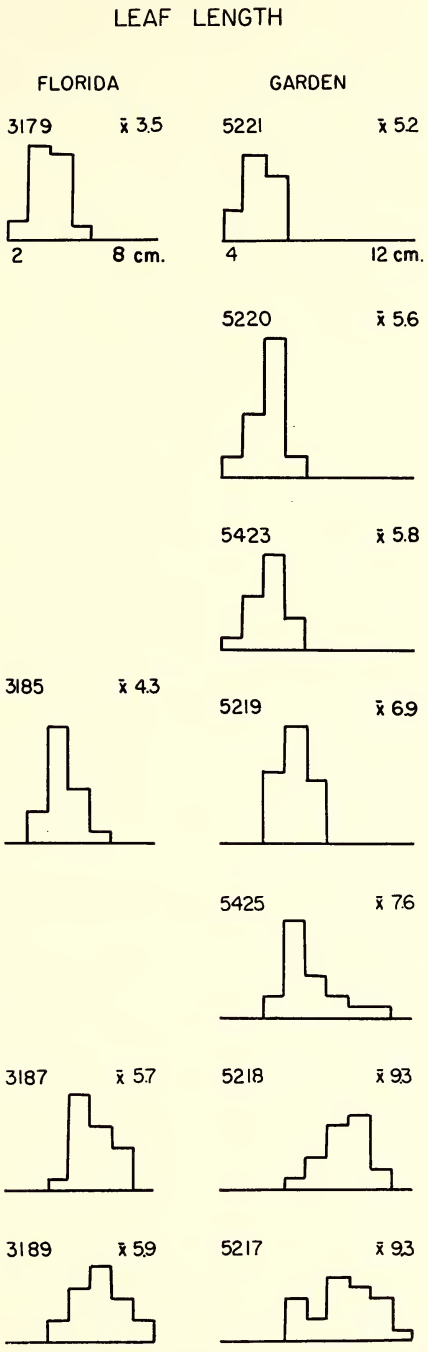

FIG. 4. Variation in leaf length of *Helianthus debilis* subsp. *debilis*.

not seem unlikely that such a habit could have originated independently in these three taxa. Both geographically and morphologically this subspecies is intermediate between subsp. *debilis* and subsp. *tardiflorus,* although in the sum total of its morphological features it appears to be more closely related to subsp. *tardiflorus*. Four populations were studied in detail both in the experimental garden and from population samples in nature, and although there is considerable variability there is no evidence of clines or of hybridization with other subspecies.

This subspecies is, like all other taxa in this species, characterized by red-purple disk flowers. It is of interest to note that one plant (5214-15) grown in the experimental garden had yellow disk flowers. Yellow disk flowers are known in *H. annuus* and *H. Bolanderi* and this character is recessive to red-purple disk flowers. The origin of the yellow disk flowers in subsp. *vestitus* is probably more readily explained on the basis of independent mutation rather than hybridization.

Flowering material has been collected in the field from January through October. In the experimental garden it comes into flower late in July.

3. Helianthus debilis subsp. **tardiflorus** subsp. nov. Herba annua ramosissima caulibus erectis glabris vel sparse hispidis maculatis vel rubris 60–75 cm. altis foliis inferioribus deltoideo-lanceolatis raro ovalibus cordatis irregulariter serratis interdum crispatis laminis 5–10 cm. longis 3–9 cm. latis pedunculis 10–25 cm. longis disci diametro 1.4–1.5 cm. phyllaribus 2–3 mm. latis ligulis 13–19, 1.4–1.6 cm. longis 6–8 mm. latis paleis hispidis.

Distribution and citation. In isolated colonies on sandy beaches in western and northern coastal Florida in Franklin, Levy, and Sarasota counties (fig. 2). Single plants of this subspecies were found in Alachua County (*Heiser 3218*) and Taylor County (*Heiser 3219*), and it was collected by Small and De Winkeler in 1919 (*9169*) in Okeechobee County, although I failed to find it in this county in 1951.

Type. Sarasota County, Sarasota Key, *Curtiss 1455,* MO.

This subspecies is most readily recognized by its usually deeply and irregularly serrate leaves (fig. 6). It also has a more bushy habit than the other subspecies because of its tendency toward abundant branching near the base. It appears to be most closely related to subsp. *silvestris,* and at one time the distribution of these two subspecies may have been continuous across the gulf coast, although today they are separated by a considerable distance (fig. 2). Crosses between subsp. *silvestris* and subsp. *vestitus* give F_1 plants which are erect and very similar to subsp. *tardiflorus* in appearance.

The three populations of this subspecies which have been studied in detail show rather conspicuous differences in type of branching, leaf length, degree and nature of leaf serration, ray number and peduncle length (fig. 5). Although these differences are maintained in cultivation, they do not seem to be sufficient basis for recognizing three taxa.

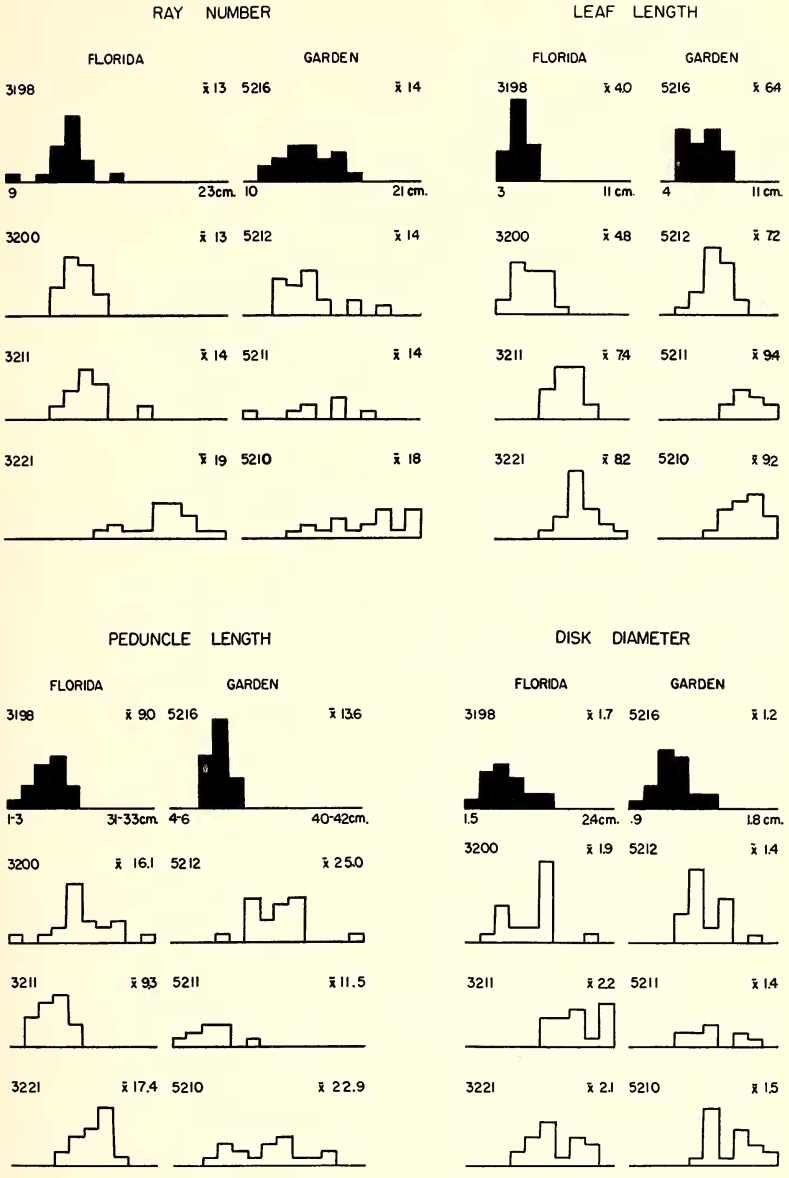

FIG. 5. Variation in four characters in *Helianthus debilis* subsp. *vestitus* (black) and *H. debilis* subsp. *tardiflorus* (white). The collections and seeds come from the following localities in Florida: *3198, 5216,* Long Beach, Sarasota Connty; *3200, 5212,* Sarasota, Sarasota County; *3211, 5211,* Cedar Key, Levy County; *3221, 5210,* Carabelle, Franklin County.

Although both subsp. *tardiflorus* and subsp. *vestitus* occur in the Sarasota region, the two do not come into contact and there is no clear-cut evidence of hybridization. However, it can be seen from figure 5 that the Sarasota population of subsp. *tardiflorus* closely approaches subsp. *vestitus* in leaf length, and disk diameter. Such evidence might suggest that there had been past hybridization between these two taxa in this region, but the measurements of peduncle length do not support this, for the Cedar Key population of subsp. *tardiflorus* which is well isolated today from subsp. *vestitus* shows the short peduncles similar to those of subsp. *vestitus,* whereas the Sarasota population of subsp. *tardiflorus* has long peduncles.

In nature flowering material of this species has been collected from March to September. In the experimental garden it matures extremely late (August and September) and several plants from Cedar Key (*5211*) were killed by frost before flowering. It seems possible that at times it may live through the winter in Florida, a fact which could account for specimens collected in flower in March.

4. Helianthus debilis subsp. **silvestris** subsp. nov. Herba annua caulibus erectis atro-rubris vel maculatis plerumque glabratis superne ramosis ramis aliquantum pendulis foliis inferioribus deltoideo-ovatis cordatis plerumque regulariter serratis laminis 6–14 cm. longis 4–13 cm. latis pedunculis gracilibus 16–30 (–40 raro) cm. longis disci diametro plerumque 1.5 cm. phyllaribus ca. 2 mm. latis ligulis 12–14 (–20 raro) 1.5–2.3 cm. longis 0.7–1.2 cm. latis paleis plerumque hispidis.

Distribution and citation. In the pine and oak regions of northeastern Texas from Shelby County to Wood County south to Waller County and Milam County (fig. 3). Upshur County: *Reverchon 2581.*

Type. Nacogdoches County: 3 miles south of Nacogdoches on U. S. Highway 59, *Heiser 3086,* IND.

This subspecies is distinguished from the others by the large, almost invariably cordate, leaves (fig. 6), the pendulous branches which arise in the upper half of the plant, and the usually rather small heads. However, one population from Houston County (*Heiser 3048*) has rather large heads and many rays. The plants of this subspecies from the northern part of its range appear to be most closely related to subsp. *tardiflorus,* and like subsp. *tardiflorus* this subspecies matures late in the experimental garden. However, in nature it has been collected as early as May. The southern limit of the subspecies has been drawn somewhat arbitrarily, in part because herbarium material from this area is scanty and also the specimens are somewhat fragmentary. Some of the specimens from the southern part of the range approach subsp. *cucumerifolius,* and it may be that hybridization between the two subspecies occurs. Such might be expected since there are no known barriers to interbreeding and the hybrids are fertile.

Another factor which may influence the variation pattern is hybridization with *H. annuus.* Hybrids have been found in Henderson County

and *H. annuus* is rather common in the southern part of the range of subsp. *silvestris* (Heiser, 1951). Although no evidence for introgression of *H. annuus* was cited previously (Heiser, 1951), it now appears that such introgression might account for the high ray number, large disks, and

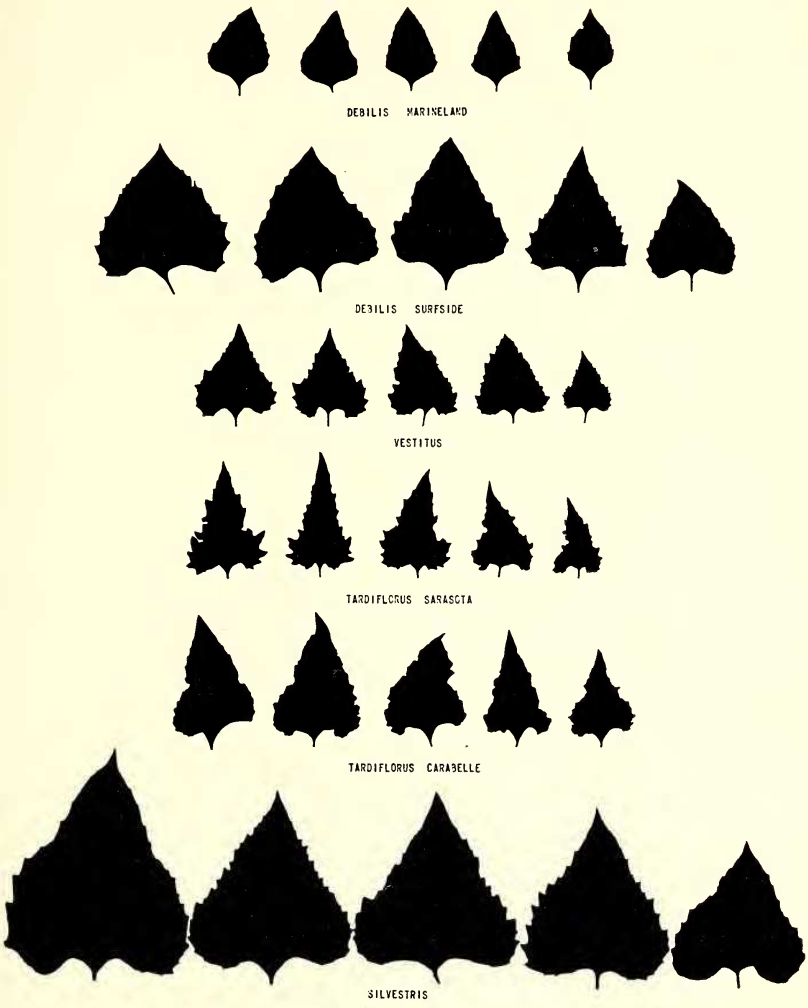

FIG. 6. Leaf outlines of *Helianthus debilis* from plants grown in the experimental garden. Leaves were selected from five plants in each population in order to show the range of variation. *H. debilis* subsp. *debilis,* Marineland, St. John's County, Fla., *5150*; *H. debilis* subsp. *debilis,* Surfside, Dade County, Fla., *5217*; *H. debilis* subsp. *vestitus,* Indian Rocks Beach, Pinellas County, *5214*; *H. debilis* subsp. *tardiflorus,* Sarasota, Sarasota County, Fla., *5211*; *H. debilis* subsp. *tardiflorus,* Carabelle, Franklin County, Fla., *5210*; *H. debilis* subsp. *silvestris,* Grapeland, Houston County, Texas, *5162*. × 1/5.

perhaps the large leaves found in some populations of subsp. *silvestris* (Heiser, 1951, Table 2).

5. Helianthus debilis subsp. **cucumerifolius** (T. & G.) stat. nov.[3] *H. cucumerifolius* Torrey and Gray, Fl. N. Am. 2:319. 1842. *H. debilis* var. *cucumerifolius* A. Gray, Syn. Fl. 1[2]:273. 1884.

Annual, much branched, branches ascending, stem hispid below, usually conspicuously purple mottled, 55–65 cm. tall; lower leaves deltoid-ovate to deltoid-lanceolate, cuneate, truncate, or cordate at base, fairly regularly serrate, slightly wavy, margined, blade 4.0–9.0 cm. long, 3.0–8.0 cm. wide; peduncles not conspicuously slender, 25–50 cm. long, disk 1.6–rarely 2.0 cm. long, 7–12 mm. broad; central pales of the chaff with hispid or slightly villous tips.

Distribution. In open sandy soils in southeastern Texas from Travis County, south to Victoria and Frio counties (fig. 3). Guadalupe County: *E. J. Palmer 11650*.

Type. Texas. Exact locality unknown. *Drummond 171,* NY.

On the whole this subspecies appears more similar to subsp. *runyonii* than to any other subspecies of *H. debilis,* although it may intergrade with subsp. *silvestris* in the northern part of its range. There is within the subspecies considerable variation which remains to be analyzed carefully. In the northern part of its range the chaff tips are generally merely hispid, in the central part of the range both hispid and slightly villous chaff tips are found, whereas in the southern part of the range generally all of the plants have slightly villous chaff tips, approaching the condition found in subsp. *runyonii* and subsp. *hirtus*. Hybridization between the subspecies, of course, is one possible explanation of this variation. This subspecies also hybridizes with *H. annuus* and it is possible that introgression from this species is another source of variability, although as yet we have no clear evidence for it.

This subspecies matures early, coming into bloom in the experimental garden in the middle of June. Flowering specimens from nature have been collected from April to October.

6. Helianthus debilis subsp. **praecox** (Engelm. & Gray) stat. nov. *H. praecox* Engelm. & Gray, Boston Jour. Nat. Hist. 5:221. 1847. *H. debilis* var. *praecox* A. Gray in Torr., Emory, Rep. U.S.—Mex. Bound. (Bot.), 90. 1859. (The Schott specimen cited by Gray is subsp. *cucumerifolius*.)

[3] *Helianthus lindheimerianus* of Scheele (Linn. 22:159. 1849) has been placed in synonymy with *H. cucumerifolius* by Watson (1929). Scheele's description might refer either to *H. annuus* or to *H. cucumerifolius*. His statement that this plant is perennial further complicates matters, but this is probably an error. For his type he cites *Lindheimer,* Neubraunfels, Texas, August, 1846, but does not give a collection number. Lindheimer's No. 96, which is *H. debilis* subsp. *cucumerifolius,* was collected at this locality, but does not agree as to date. His *H. annuus* No. 259 does agree, however, and therefore I am inclined to consider *H. lindheimerianus* as synonymous with *H. annuus* subsp. *texanus* Heiser.

Annual, usually somewhat prostrate or erect with branches horizontal, stem greenish, not conspicuously mottled, hispid to hirsute, 40–50 cm. tall; lower leaves deltoid-ovate, usually cuneate to truncate at base, finely and fairly regularly serrate, 3.0–8.0 cm. long, 2.0–7.0 cm. wide; peduncles 15–30 cm. long; disk about 1.4 cm. in diameter; phyllaries 3–4 mm. broad, short-attenuate; rays generally 14–15, 1.7–2.7 cm. long, 7–12 mm. broad; central pales of the chaff hispid or occasionally slightly villous.

Distribution and citation. In coastal sands on Galveston Island, Texas, and adjacent mainland in Galveston and Chambers counties (fig. 3). Chambers County: *Cory 51022*.

Type. Texas. Galveston County, Galveston Island, *Lindheimer 97*, MO.

This taxon was originally described as a species, but later Gray reduced it to synonymy under *H. debilis*. Watson (1929, p. 355) states that the type of *H. praecox* should be referred to *H. petiolaris*, and the description to *H. debilis*. Watson has "completely misinterpreted" (to use his own words) the type specimen. The description matches the type perfectly. Watson was under the impression that the central pales of the receptacle were villous only in *H. petiolaris*.

The semi-prostrate habit and the pubescence of this subspecies suggest an affinity to subsp. *vestitus*, but the similarities here are in all probability the result of parallel development of coastal ecotypes in Texas and Florida. When all the morphological features are considered, the relationships of subsp. *praecox* are clearly seen to be with the southern Texas race, subsp. *runyonii*, with which it produces fertile hybrids.

Helianthus annuus appears as a weed on Galveston Island, and hybrids with subsp. *praecox* have been found in several localities.

This subspecies flowers fairly early (late June) in the experimental garden, and has been collected in nature in flower from July to November.

7. Helianthus debilis subsp. **runyonii**, subsp. nov. Herba annua caulibus erectis plerumque rubris hispidis vel hirsutis 50–60 cm. latis foliis inferioribus deltoideo-ovatis basi cuneatis vel truncatis plerumque dentibus parvis acutis regulariter serratis laminis 3.0–7.5 cm. longis 2.0–6.0 cm. latis pedunculis 20–30 cm. longis disci diametro ca. 1.4 cm. phyllaribus 3–4 mm. latis abrupte attenuatis ligulis plerumque 11–13, 2.2–2.4 cm. longis 1.0–1.1 cm. latis paleis florium disci centralium villosis.

Distribution and citation. Coastal prairies from Aransas County to Cameron County, Texas (fig. 3). San Patricio County: *Whitehouse 18133*.

Type. Willacy County, Yturria, *Robert Runyon 4365*, IND.

Morphologically this subspecies is intermediate between subsp. *praecox* and subsp. *hirtus*, the two races with which it produces fertile F_1 hybrids. In the northern part of its range there is some difficulty in distinguishing this subspecies from subsp. *cucumerifolius*, and additional field study needs to be undertaken. The specimens from Brooks County (*Ferris* and

Duncan 3200, Tharp 3834) are somewhat more robust than the other specimens and have thicker leaves. Hemsley (Biol. Cent. Am. 2:180. 1881–1882) lists *H. praecox* from northern Mexico based on the collection of Berlandier, no. *2354*. I have not seen this specimen, but it may well be *H. debilis* subsp. *runyonii*.

This subspecies flowers fairly early (late June) in the experimental garden, and has been collected from April to November in Texas.

8. Helianthus debilis subsp. **hirtus,** subsp. nov. Subspeciei runyonii similis sed hirsutior laminis 3.0–9.0 cm. longis 2.0–7.0 cm. latis pedunculis 30–40 cm. longis disci diametro 1.5–1.7 cm. ligulis 14–16, 2.1–2.7 cm. longis 0.7–1.3 cm. latis.

Distribution. Known only from near Carrizo Springs, Dimmit County, Texas (fig. 3).

Type. Texas. Dimmit County, Carrizo Springs, *Heiser 3064,* IND.

This local race is most distinctive because of the hirsute pubescence. It has previously been confused with *H. petiolaris,* and Watson has annotated specimens of it as such. Its relationship to *H. debilis* is most clearly seen in the leaves (fig. 7), and in its crossing relation it has been shown to belong to the "praecox" assemblage of *H. debilis*. In its chaff pubescence, however, it is almost identical to *H. petiolaris*. After three generations of crossing sister plants from this population (*3064*), progeny has been obtained with almost glabrous chaff. The latter species does not occur in this area, but *H. annuus* does and hybridizes with subsp. *hirtus*. However, the peculiar features of subsp. *hirtus* almost certainly are not derived from *H. annuus*.

This subspecies is apparently confined to a single population. It is of interest to note that the Carrizo Springs sand region is also the home of a number of other endemics (Shinners, oral communication). The pocket gophers also have a subspecies limited to this same small area (Davis, 1940).

Subspecies *hirtus* flowers relatively early in the experimental garden, and flowering plants have been collected in nature from April through July.

Helianthus debilis as a Weed

Helianthus debilis makes its appearance as a weed in a number of localities in the eastern United States outside of Florida and Texas. Apparently in most localities where it has been reported, it is merely locally established, frequently as an escape from cultivation. However, in Georgia and South Carolina it forms extensive colonies along roadsides and is well established as part of the weedy flora. The decision as to whether these plants are indigenous in these states or represent introductions from either Florida or Texas rests on the following evidence. In Texas and in Florida *H. debilis* occurs in a number of places which are relatively undisturbed by man, whereas in Georgia and South Carolina the plants occur only as

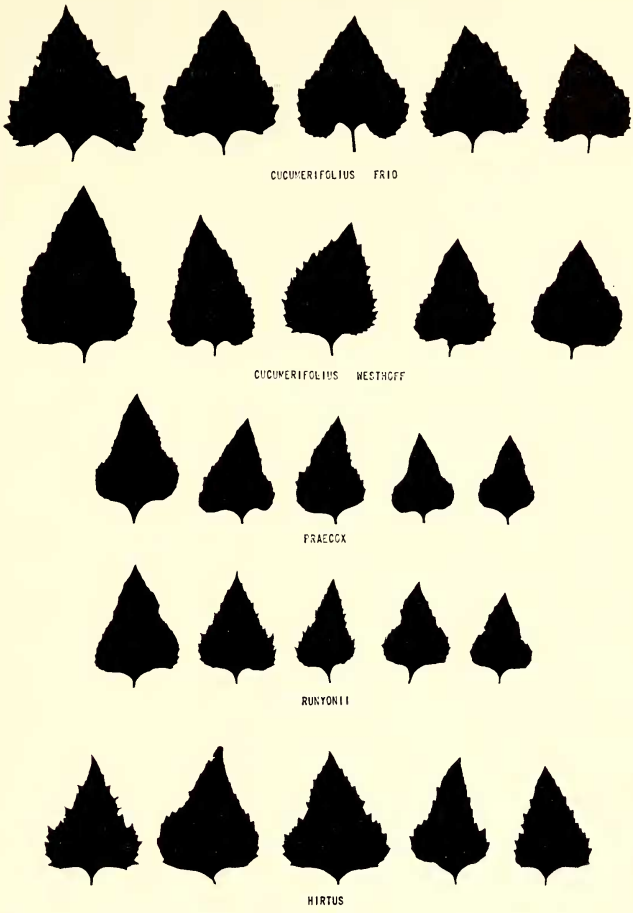

FIG. 7. Leaf outlines of *Helianthus debilis* from plants grown in the experimental garden (cont.). *H. debilis* subsp. *cucumerifolius,* Frio, Dilley County, Texas, *5161*; *H. debilis* subsp. *cucumerifolius,* Westhoff, DeWitt County, Texas, *5156*; *H. debilis* subsp. *praecox,* Galveston Island, Galveston County, Texas, *5159*; *H. debilis* subsp. *runyonii,* Yturria, Willacy County, Texas, *5160*; *H. debilis* subsp. *hirtus,* Carrizo Springs, Dimmit County, Texas, *5158*. × 1/5.

roadside weeds. Secondly, *H. debilis* was not collected in the latter states until 1899 (*Cuthbert*) whereas the species was collected in both Florida and Texas before 1850. Moreover, the Cuthbert collection from Georgia has "escape" written on some of the sheets.

From their geographical position one might suppose that these weed races in Georgia and South Carolina were introduced from Florida, but all in all the weed specimens seem to have more in common with subspecies *cucumerifolius* of Texas. However, the weed specimens differ from this subspecies in their larger disks (1.7–2.0 cm. in diam. at anthesis), and larger leaves (9–12 cm. long, 8–11 cm. wide) which are almost invariably

cordate at the base. For the present I do not feel that it is necessary to give the weeds a distinct epithet, but simply refer them to *H. debilis* subsp. *cucumerifolius*. Both the large heads and leaves could have been derived through introgression from *H. annuus*. Furthermore, segregates with a yellow disk have appeared among plants grown in the experimental garden; this also suggests influence from *H. annuus*.

Distribution. Connecticut: Fairfield County, New Haven County, New London County. Massachusetts: Barnstable County. Pennsylvania: Lehigh County. Virginia: Isle of Wight County. North Carolina: Sampson County, Pender County. South Carolina: Florence County, Aiken County. Georgia:[4] Taylor County, Richmond County. Alabama: Houston County. Louisiana: Calcasieu Parish, Rapides Parish.

Ornamental Races

Helianthus debilis is grown as a garden ornamental and is carried by a number of seed companies in the United States and Europe. Without much doubt it is the most attractive annual species of the genus. A number of strains have been grown both at Bloomington and in St. Louis. There is considerable variation between strains, particularly in regard to ray color, which varies from a pale primrose to a deep orange yellow; morphologically most of them resemble either subsp. *cucumerifolius* or subsp. *silvestris*. Some of the ornamental strains are almost identical to the weeds of South Carolina and Georgia. Some seeds offered as "H. cucumerifolius" when grown proved to be *H. annuus*, and other strains show evidence of having been derived from hybrids between *H. annuus* and *H. debilis* subsp. *cucumerifolius*.

Discussion and Conclusions

For purposes of discussion we may think of *H. petiolaris*, the "debilis" assemblage (subspecies *debilis, vestitus, tardiflorus, silvestris* and *cucumerifolius*), and the "praecox" assemblage (subspecies *praecox, runyonii* and *hirtus*) of *H. debilis* as three incipient species. It seems highly probable that they all have come from a recent common ancestor. The morphological differentiation that has occurred can perhaps most readily be explained by geographical isolation which has permitted the development of different gene combinations in response to different environmental conditions. Partial reproductive barriers leading to some sterility in F_1 hybrids appear to have developed through structural changes in the chromosomes. The incipient speciation in these sunflowers then can be readily explained in neo-Darwinian terms. In attempting to reconstruct the past history of this group we are hampered by the lack of any fossil evidence and of any indication of the ages of the various racial components, factors which make it exceedingly difficult to explain the present distribution. It is known, however, that the region inhabited by *H. debilis* is for the most part quite young geologically. In the following discussion certain assump-

[4] Thorne (Castanea 16:29. 1951) also reports it from Clay and Seminole counties.

tions are made. The principal ones are rather obvious: (1) races having the same structural arrangement of chromosomes as indicated by pairing at meiosis come from the same progenitor, and (2) in general, morphological similarities indicate closeness of relationship. Moreover, we shall speak of certain types as the progenitor or original type, although it is fully realized that in all probability no existing race is similar to the progenitor.

It has been shown on morphological grounds that *H. debilis* subsp. *hirtus* connects "praecox" to *H. petiolaris* and that subsp. *runyonii* connects "praecox" to "debilis" by way of subsp. *cucumerifolius*. From the crossing studies it has also been shown that "praecox" forms a bridge between "debilis" and *H. petiolaris*. Assuming that one of these three is similar to the progenitor we have the following possibilities: (1) *H. petiolaris* could have been the progenitor which gave rise to "praecox" which in turn gave rise to "debilis." This would imply a western origin and then a gradual spread over the newly arisen land in the gulf coast region sometime in the Miocene or later. In this connection it should be pointed out that five other annual sunflowers today are centered in the western United States, whereas only two species are native to the gulf region. (2) The second possibility is that "praecox" is the original type which in turn gave rise to *H. petiolaris* to the west and "debilis" to the north and east. (3) From the evidence we have it is equally likely that a subspecies of the "debilis" assemblage could have been the ancestral type which gave rise to "praecox" and that "praecox" in turn gave rise to *H. petiolaris*. Thus it can be seen that no definite conclusions can be reached in regard to the progenitor.

A second problem is to explain the origin of subsp. *debilis,* which has been shown to differ greatly morphologically from the remainder of the species. Such great morphological differentiation might be explained by an early isolation of the progenitor of this subspecies from the ancestral species. One is tempted to postulate long-distance dispersal of *H. debilis* into Florida in the lower Oligocene when Florida appeared as an island isolated from the mainland (Schuchert, pl. 11, 1935) and later a gradual spread of subsp. *vestitus* and subsp. *tardiflorus* into peninsular Florida from the northwest.

In view of the fact that the differences between subsp. *debilis* and the other subspecies of the "debilis" assemblage are as great as, or greater than, the differences between "debilis," "praecox," and *H. petiolaris* in Texas we might suppose that the isolation of the ancestor of subsp. *debilis* took place before the differentiation of the other taxa. Then at some later date *H. petiolaris,* "praecox," and "debilis," excepting subsp. *debilis,* differentiated with the latter assemblage retaining the original structural arrangement of the chromosomes. If this is actually the case it means that all the other subspecies of "debilis" are more closely related to "praecox" and *H. petiolaris* in terms of a recent common ancestor than to subsp. *debilis*. If these crossing groups were interpreted as species it

can be seen that it might give us an unnatural classification. To follow this to its logical conclusion we might point out that the use of sterility or crossing limits, which is the primary prerequisite in most genetic species definitions, may actually obscure understanding relationship at times.

Thus far, in order to complicate the discussion as little as possible, no consideration has been given to the possibilities of hybridization in attempting to explain the evolution of these sunflowers. It is difficult to evaluate the role of hybridization, particularly since it may go hand in hand with the other mechanisms promoting evolution, but it has almost certainly played a role.

It has been pointed out repeatedly that "praecox" is intermediate between *H. petiolaris* and "debilis," and although the latter two are not known to hybridize today it is possible that past hybridization could have taken place which gave rise to "praecox." Unfortunately, few crosses have been made between *H. petiolaris* and "debilis," but in those which have been made, the F_1 progeny would most nearly key out to "praecox" although they do not exactly match any of the existing three subspecies. The artificial F_1 has reduced fertility, but it seems possible that stable, fertile types might be selected from hybrid derivatives of *H. petiolaris* and "debilis" which would differ both morphologically and in chromosome structure from the parental types.

There also exists the possibility that certain of the subspecies owe their origin at least in part to hybridization. *Helianthus annuus* is known to hybridize naturally with several of the subspecies. Although in an earlier paper (1951), wherein all Texas races of *H. debilis* were referred to *H. debilis* var. *cucumerifolius,* it was stated that there was no evidence of introgression of *H. annuus* into "debilis," it now seems probable that genes from *H. annuus* might account for the large disks, numerous rays, and large cordate leaves of certain Texas populations of subsp. *silvestris*. It has also been pointed out that subsp. *tardiflorus* in some respects is intermediate between subsp. *silvestris* and subsp. *vestitus,* although from present-day distribution one can hardly postulate hybridization to explain the origin of subsp. *tardiflorus*. Other possibilities of hybridization modifying the subspecies have been pointed out in the section on taxonomy.

The foregoing discussion has explored some of the possibilities which might account for the present pattern of subspeciation in *H. debilis*. However, we cannot satisfactorily point to one taxon as the definite progenital type, nor can we evaluate fully the role of hybridization. In a group of closely related diploid organisms in which nothing is known of the past history of the taxa, and many times when it is, it is practically impossible to construct a phylogenetic "tree." On the other hand, it has been possible to show the relationships of the various taxa as they exist today using the criteria of comparative morphology and crossability.

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A NEW TRIFOLIUM FROM OREGON

Helen M. Gilkey

In May of 1954, Mrs. Bessie Fleischman Murphy, an analyst at the Seed Laboratory located at Oregon State College, discovered in southeastern Oregon a colony of a conspicuous large-headed clover, specimens of which she brought to the writer for identification. It proved strikingly different not only from any species previously known in the state but, so far as could be determined, from any thus far described. Consequently it is offered here as new to science.

In size of head, this species is comparable, in northwestern United States, only to *Trifolium macrocephalum* (Pursh) Poir. and *T. Thompsoni* Morton. But resemblance to either of these species ceases with this character. In fact the new clover is barred, by its possession of only three leaflets, from the section Macrocephala to which these two species are assigned.

The single colony located by Mrs. Murphy represents practically a pure stand, though the plants are scattered. It occurs in Malheur County on a bluff above Sucker Creek, a tributary of Snake River, in a section where fingers of coarse-textured blue-gray diatomaceous earth protrude into the darker soil of typical sagebrush plains. The new clover occurs only upon these light-colored areas, its glaucous herbage blending closely with the blue-gray soil. Except upon this slope which is pre-empted by the clover, *Artemisia tridentata* is the predominant species in the region.